**Soil fauna through the landscape window: factors shaping surface-and soil-dwelling communities across spatial scales in cork-oak mosaics**

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Pedro Martins da Silva • Matty P. Berg • António Alves da Silva • Susana Dias • Pedro J. Leitão • Dan Chamberlain • Jari Niemelä • Artur R.M. Serrano • José Paulo Sousa

P. Martins da Silva (corresponding author) • A. A. da Silva • J. P. Sousa

MARE - Marine and Environmental Research Centre, Department of Life Sciences, University of Coimbra, Largo Marquês de Pombal, 3004-517 Coimbra, Portugal
E-mail: pgpmartins@yahoo.co.uk
Phone: +351 239836386; Fax: +351 239823603

M. P. Berg • P. Martins da Silva
Department of Ecological Science, VU University, Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, Netherlands

S. Dias • P. J. Leitão
Centre for Applied Ecology Prof. Baeta Neves, Institute of Agronomy, Technical University of Lisbon, Tapada da Ajuda, P-1349-017 Lisbon, Portugal

P. J. Leitão
Geomatic Lab, Geography Department, Humboldt-Universität zu Berlin, Rudower Chaussee 16, 12489 Berlin, Germany

D. Chamberlain
Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy

J. Niemelä

Department of Environmental Sciences, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland

A. R. M. Serrano • P. Martins da Silva
Centre for Environmental Biology, Faculty of Sciences, University of Lisbon, Rua Ernesto de Vasconcelos Ed. C2-2ºPiso, Campo Grande, 1749-016 Lisbon, Portugal

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**Abstract**

Context. The role of spatial and environmental processes governing community structure are dependent on the spatial distances among local communities and the degree of habitat heterogeneity at a given spatial scale. Also, they depend on the dispersal ability of the targeted organisms collected throughout a landscape window.

Objectives. Here we assessed the relative importance of spatial and environmental factors shaping edaphic (Collembola) and epigeous (Carabidae) communities at different scales.

Methods. The sampling sites were four different landscape windows (1km$^2$ square each) in a Mediterranean cork-oak landscape in Portugal. Variance partitioning methods were used to disentangle the relative effects of spatial variables (MEMs, e.g. patch size, shape and configuration) and environmental variables across spatial scales (habitat: data on % of vegetation cover types; management: data on forestry and pasture interventions; landscape: data on landscape metrics).

Results. The relative effects of environmental and spatial factors at different scales varied between Collembola and Carabidae. The pure effect of the environmental component was only significant for carabid beetles and explained a higher percentage of their community variance compared to to collembolan communities. The pure effects of the spatial component were generally higher than the environmental component for both groups of soil fauna. Carabid communities responded to landscape features related to the patch connectivity of open areas (grasslands) as well as the shape of cork-oak habitat patches integrating the agro-forest mosaic.

Conclusions. Community patterns of surface-dwelling soil fauna may be partly predicted by some features of the landscape, while soil-dwelling communities require ecological assessments at finer spatial scales.

**Keywords:** Community structure; Cork-oak landscape; Dispersal ability; Environmental factors; Soil fauna; Spatial scale.

## Introduction

Community structure within landscape mosaics is influenced by ecological processes operating at a hierarchy of spatial scales, from local environmental filtering to the regional movement of species among habitat patches (Ricklefs 1987; Myers et al. 2013). The relative influence of environmental and spatial processes may also depend on the home range and dispersal ability of the targeted organisms (Cottenie 2005; Thompson and Townsend 2006; van de Meutter et al. 2007; Heino 2013).

In terrestrial environments, only a limited number of ecological studies have focused on soil fauna to test the relative effects of environmental and spatial factors, mostly on epigeous beetles (e.g. Davies et al. 2009; Driscoll et al. 2010; Boieiro et al. 2013), but also a few studies on soil microarthropods, namely mites (Lindo and Winchester 2009; Bowler and Benton 2011), collembolans (Aström and Bengtsson 2011; Martins da Silva et al. 2012), or both (Chisholm et al. 2011; Ingimarsdóttir et al. 2012). Soil fauna in fact comprise an interesting group to test this ecological question, given their diverse array of dispersal abilities (Hopkin 1997; Ojala and Huhta 2001; Ponge et al. 2006). Soil organisms are generally small, with a limited home range and poor dispersal ability compared to aboveground organisms (Hedlund et al. 2004; Rantalainen et al. 2005). However, large differences in terms of life-traits, such as the vertical distributions in soils (life-forms), exist between different groups of soil organisms and may underlie their movements and distributions throughout heterogeneous landscapes (Lindberg and Bengtsson 2005; Ponge et al. 2006; Vandewalle et al. 2010; Querner et al. 2013). For instance, a significant proportion of carabid beetle species (Coleoptera, Carabidae) are epigeous and can fly (e.g. Desender and Turin 1989; Lövei and Sunderland 1996), while collembolan communities (Collembola) are generally dominated by eu-edaphic and hemi-edaphic species (soil

dwelling communities), and are very restricted in dispersal ability (e.g. Bengtsson et al. 1994).

Besides spatial limitation, the heterogeneity of habitat patches, their shape and configuration within the landscape mosaic are perceived differently by species differing in body size and vertical distribution in soils (Ettema and Wardle 2002; Chust et al. 2003a; Bardgett et al. 2005). Larger, epigeous organisms, especially predators, generally need larger habitat areas to fulfill their niche requirements (Chust et al. 2003b; Schuldt et al. 2013), and changes in their community structure may be related to habitat fragmentation and landscape configuration at a broad spatial scale (e.g. Martins da Silva et al. 2008; Diekötter et al. 2010; Woltz et al. 2012). The distribution of smaller, eu-edaphic fauna, on the other hand, is more constrained by soil habitat heterogeneity at finer-grained spatial scales due to their limited home range and dispersal ability (Bengtsson et al. 1994; Ettema and Wardle 2002; Berg and Bengtsson 2007). Eu-edaphic soil communities are then expected to exhibit a more patchy distribution in comparison to epigeous communities (such as carabid beetles) occurring in the same landscape mosaic. Nonetheless, recent studies have indicated the importance of broad-scale landscape processes in governing soil fauna community structure (Querner et al. 2013), for instance by constraining local habitat conditions verified at finer spatial scales (Martins da Silva et al. 2012; Heiniger et al. 2014).

Although researchers have increased their awareness of the fact that ecological processes occur across a range of defined spatial scales (e.g. Sattler et al. 2010; Flohre et al. 2011; Sarthou et al. 2014), the multi-scale effects of landscape complexity at a broad scale and local habitat features at a fine-scale remain poorly understood. Also, despite that the effects of spatial and environmental factors at different scales might differ across taxonomic groups that vary in home range and dispersal ability, only a few

attempts at comparative studies have been carried out, mostly using aquatic fauna in ponds and streams (e.g. Beisner et al. 2006; Thompson and Townsend 2006; van de Meutter et al. 2007; Siqueira et al. 2012; Heino 2013).

In this study, we analyzed changes in community structure of collembolans (soil dwelling, small-bodied, low dispersal ability) and carabid beetles (surface dwelling, relatively large-bodied and high dispersal ability) in a typical Mediterranean landscape mosaic of extensive managed pastures interspersed with cork-oak woodlands. Our first hypothesis is that the relative importance of spatial processes differs between epigeous and eu-edaphic fauna. We predict that distances separating cork-oak woodland habitats have a higher effect on collembolans than on carabid beetles, due to the lower home range and dispersal ability of the former. Our second hypothesis is that environmental processes occurring at different spatial scales determine communities with different life-forms. We predict that environmental factors at coarser spatial scales, namely patch shape and configuration at the landscape scale, will more distinctly determine carabid beetle community structure in relation to the eu-edaphic communities.

## Materials and methods

*Study area and sampling design*

Field sampling was conducted in a typical Mediterranean cork-oak (*Quercus suber* L.) agro-forest mosaic, located in the consolidated alluvial plain of the river Tagus, in "Companhia das Lezírias" (Alcochete) - 20km east of Lisbon, Portugal (ca. 38º 53' N, 08º 52' W) in 2002. The sampling sites were four different landscape windows (LW, 1km$^2$ each), selected along a gradient of land-use management, from unmanaged woodland (LW1) to areas subjected to traditional management practices, such as forestry (LW2, LW3 and LW4) and pastures (LW3 and LW4). Thus, while LW1 and

LW2 were dominated by closed cork-oak woodlands, in LW3 and LW4 open woodlands and pasture lands were predominant (Table 1, see for more details Sousa et al., 2004). These landscape windows were selected in a former project (BIOASSESS: http://www.nbu.ac.uk/bioassess/) to study the effects of land-use gradients on diversity and ecological indicators. Sampling in each LW was carried out in a regular grid of 16 plots (4 by 4 plots) 200m apart (Fig. 1).

At each plot, collembolan communities were sampled by taking one soil core of 5 cm diameter in spring (May to June). Collembolans were extracted by the Macfadyen extraction method (Sousa et al. 2004). Carabid beetles were sampled in spring and autumn (September to October). They were collected using four unbaited pitfall traps (filled with ethylene glycol to preserve the animals) at each plot, placed in a quadrat with 5 m between each pitfall (Martins da Silva et al., 2008). Collembolan and carabid species were identified to the species level using appropriate identification keys.

*Species data*

The total number of sampling points used in the analyses was 60 points of a potential total of: 4x4x4=64 points (from LW1, 2, 3 and 4). Four points (L3P5, L3P9, L4P13 and L4P3) had no data for Collembola. As such, and in order to make the results even more comparable, only the 60 points were used for both Collembola and Carabidae.

The species data were Hellinger transformed to make it suitable for the use of linear ordination methods (Legendre and Gallagher 2001). Species data transformation was calculated using the function “decostand” from the "vegan" package (Oksanen 2013) in R 3.0.1 software (R Core Team 2013).

*Environmental variables across scales*

144 The effects of environmental conditions in the local plots versus the importance of
145 distances separating cork-oak habitats across LWs, as well as the relative importance of
146 local habitat, patch management and aspects of landscape structure (landscape metrics)
147 on collembolan and carabid beetle community changes, were evaluated.

148 To analyze the relative importance of environmental factors at different scales,
149 we adopted the plot-patch-landscape approach according to Cushman and McGarigal
150 (2002). The concept was implemented and a dataset for each level was defined *a priori*
151 for this study.

152 At the plot-level (habitat dataset), plot variables were the percentage soil cover
153 by litter, lichens, mosses, herbs, low shrubs, tall shrubs and trees (Martins da Silva et
154 al., 2012; Table A1).

155 At the patch-level (management dataset), management type was measured by
156 several parameters of management intensity, namely forestry practices (e.g. cork-oak
157 area with cork production and time since last cork removal) and agricultural practices
158 (e.g. Cattle stock density and number of grazing days) (Table A1).

159 At the landscape level (landscape dataset), the landscape features were patch
160 composition and configuration metrics calculated for each patch type (cork-oak
161 woodland - F, shrub lands – S, pasture lands – G) in FRAGSTATS 3.3 (McGarigal et
162 al., 2002), which were extracted from aerial photographs using ArcView software
163 (version 3.x, ESRI, US). After exploratory factor analysis, performed to exclude highly
164 collinear landscape variables, we selected eight landscape metrics for each patch type
165 existing within each LW, namely four area/density metrics (total area - AREA, mean
166 patch area - AreaMN, number of patches – NP, and radius of gyration - GYRATE) and
167 four shape/configuration metrics (shape index – SHAPE, related circumscribing circle –

CIRCLE, contiguity index – CONTIG, and proximity index - PROX) (for a detailed description of each metric see McGarigal et al. 2002 and Table A1).

Forward selection of the environmental variables was performed separately for each dataset (i.e. habitat, management and landscape datasets), using double stopping criteria (Blanchet et al. 2008). In this method, the forward selection stops when the fixed threshold for the alpha significant level ($\alpha$=0.05) or the adjusted coefficient of multiple determination ($R^2_{adj}$) of the full model is reached. The forward selection was performed using the "packfor" package (Dray et al. 2013) in R 3.0.1 software (R Core Team 2013).

*Spatial modelling*

The spatial coordinates (UTM coordinate system) were Euclidean-centered prior to the spatial data analysis.

Moran's eigenvector maps (MEM) were used to detect and quantify the spatial structure of the data. We follow the general framework described by Dray et al. (2006) that define the spatial weighting matrix W as a Hadamard product of the connectivity matrix B by the weighting matrix A. In our analysis, we used a binary (unweighted) spatial matrix constructed using a connectivity matrix based on a Gabriel graph (Legendre and Legendre 2012). Only the MEM eigenvectors that presented a significantly spatial autocorrelation, calculated using Moran's I test (Moran 1948; Cliff and Ord 1973), were selected for the analysis. Forward selection was performed on this set of MEM eigenvectors using double stopping criteria (Blanchet et al. 2008) to prevent incorrect variables from entering the model.

To evaluate the effect of the spatial scale, the spatial eigenfunction models were divided into two sub-models, the broad-scale and the fine-scale sub-model. These two

sub-models are orthogonal to one another and consequently it is expected that the shared explained variation will be zero. However, the current method of calculating the variation partitioning based on $R^2_{adj}$ creates small non-zero intersection values between the two sub-models. The solution adopted to deal with this problem was to consider a hierarchical partitioning of the shared fractions according to the different scales that each sub-model represents (i.e. the broad-scale sub-model has priority over the fine-scale sub-model) (Legendre et al. 2012).

Spatial eigenfunction models, namely MEM, were computed in R 3.0.1 software (R Core Team 2013) using the "spdep" package (Bivand 2013) and the "spacemaker" package (Dray 2013). Hierarchical variance partitioning was performed using the function "varpart.MEM" (Legendre et al. 2012).

*Community similarity within and among LWs*

In order to check for differences in collembolan and carabid beetle' community structure within and among LWs, we compared community similarities for the two taxonomic groups using Bray-Curtis (BC) similarity indices (Bray and Curtis 1957). BC similarity indices were calculated using PRIMER 5 for Windows (Version 5.2, Primer-E, Ltd., Plymouth, UK). The magnitude of divergence between sampling plots for both collembolan and beetle similarity matrices were estimated using Clarke's (1993) R statistic (ranging from 0 to 1), and ANOSIM was used to estimate the significance of differences between pairs of sampling plots, using 5000 permutations of the data (Clarke 1993). For this analysis, BC similarity values were log-transformed.

*Variance partitioning along the land-use gradient*

The relative importance of spatial and environmental factors at different levels (habitat, management, landscape) across taxonomic groups was analyzed by the method of variance partitioning using partial RDA analyses. The variation partitioning analysis was based on $R^2_{adj}$ statistics, which has been proven to be an unbiased method to calculate the fractions of the variation partitioning (Peres-Neto et al. 2006).

*Non-spatial model*

Variation partitioning techniques were first applied to the environmental variables in order to decompose the variance of each of the predefined levels (i.e. habitat, management and landscape) without considering the spatial component. The variation partitioning was presented graphically using a Venn diagram, and through the use of statistical tests (Monte Carlo permutations) we evaluated the significance of some of the fractions of the variation partitioning.

*Space versus Environment*

The joint and independent (pure) effects of environmental and spatial factors were also disentangled by the variance partitioning method. To extract the pure effects of spatial and environmental components, we used the respective selected environmental and spatial variables as co-variables, ruling out their relative influence on community changes (Borcard et al. 1992; Cottenie 2005).

Previously, the variation partitioning of the environmental variables was performed using the variables selected for each level (plot habitat, patch management and landscape level). Here, the hierarchical variation partitioning of the spatial component was also performed using two different spatial sub-models representing the

243 broad scale and the fine scale. Results were expressed through Venn diagrams and
244 Monte Carlo permutations as described above, for each fraction of the variation
245 partitioning, i.e. environmental (env), broad-scale (broad) and fine-scale (fine) spatial
246 components. .
247 The ordination analysis was performed using the "vegan" package (Oksanen
248 2013) in R 3.0.1 software (R Core Team 2013).
249
250 **Results**
251 *Overview on species richness and composition across LUs*
252 In total, 54 collembolan species were sampled across LWs (35, 24, 28 and 30 species in
253 LW1, LW2, LW3 and LW4, respectively), while 55 species of carabid beetles were
254 recorded (24, 20, 38 and 30 species in LW1, LW2, LW3 and LW4, respectively).
255 Overall, average dissimilarity among samples was greater among collembolan
256 communities compared to carabid communities (Fig. 2). A higher among-sample
257 divergence was found even within LWs (Fig. 2). However, differences in community
258 structure between LWs were generally stronger for carabid communities (more
259 significant R values from ANOSIM, Table 2). The exception was the pairwise
260 comparison between LW1 and LW2, showing that these two LWs were not dissimilar in
261 terms of carabid community composition and species relative abundances (Table 2).
262
263 *Variance partitioning: non-spatial model*
264 Environmental effects along the predefined levels (habitat, management and landscape)
265 were examined for both collembolan and carabid communities by means of (partial)
266 RDA analyses using the procedure of forward selection. A total of 5 and 7
267 environmental variables were selected for Collembola and Carabidae, respectively

(Table 3). The variables were selected independently for each one of the predefined levels or subsets. Consequently, the habitat level was composed of 1 variable for both Collembola and Carabidae (namely Herb), while the management and landscape levels were composed by 2 variables for Collembola (management: Density, TimeCork; landscape: G_NP, F_Contig) and 3 for Carabidae (management: AreaCork, TimeCork, AreaCut; landscape: G_Shape, F_Shape, G_Prox) (Table 3).

The variation partitioning technique applied to the environmental variables across scales showed different results between the two taxonomic groups. The pure (independent) effect of each environmental variance component was not significant for collembolan communities, while factors at the habitat and landscape scales significantly explained carabid community changes across LWs (Venn diagram in Fig. 3). Moreover, the percentage of collembolan community variance explained by environmental variables was overall very low, in absolute terms and also in comparison with carabid beetles (Fig. 3). The greater amount of community variation was explained by the fraction of the shared effect between landscape structure and patch management (3%). This same fraction also explained the higher amount of carabid community variance (7.7%), followed by the joint effect of all variables (4.6%) and the pure effect of landscape (3.3%) explaining the community changes. The most important landscape factors determining carabid beetle communities were related to patch connectivity of open areas (grasslands, G_Prox) as well as the shape of closed woodlands and more open habitats (F_Shape and G_Shape, respectively) integrating the agro-forest mosaic (Table 3).

*Spatial versus environmental effects across spatial scales*

In common with the environmental component, spatial variables were submitted to a procedure of forward selection, resulting in 7 selected variables (MEMs) for each taxonomic group, separated along broad-scale (Collembola: MEM's1, 2, 3, 35; Carabidae: MEM's 1, 2, 3, 11, 12, 18) and fine-scale sub-models (Collembola: MEM's 44, 47, 57; Carabidae: MEM 43).

The relative importance of environmental and spatial factors at different scales varied between Collembola and carabid beetles. The effect of the environmental component, after removing the effect of the space component, was only significant for carabid beetles and explained a higher percentage of their community variance (5.34%, *pseudo*-$F_{(6,46)}$=1.626, P=0.003) in relation to collembolan communities (1.12%, *pseudo*-$F_{(5,47)}$=1.134, P=0.203) (Venn diagram in Fig. 4). The pure effects of the spatial component were generally higher than the environmental component for both taxonomic groups. Total effects of the pure space component explained 6.39% (*pseudo*-$F_{(7,47)}$=1.571, P=0.003) of the collembolan species variance and 7.13% (*pseudo*-$F_{(7,46)}$=1.731, P=0.001) of carabid species variance (Fig. 4). Considering the two subsets of the spatial component, only the pure effects of the fine-scale sub-model significantly explained collembolan species variance across LWs (*pseudo*-$F_{(3,47)}$=1.997, P=0.001), while the independent effects of the broad-scale sub-model were not significant (*pseudo*-$F_{(4,47)}$=1.253, P=0.098). Conversely, both spatial sub-models showed a significant effect on carabid species variance (broad-scale: *pseudo*-$F_{(6,46)}$=1.643, P=0.002; fine-scale: *pseudo*-$F_{(1,46)}$=2.18, P=0.01), and the broad-scale subset explained a considerably higher percentage of community variance in relation to the fine-scale model (Fig. 4).

In both taxonomic groups, the shared effects of environmental and broad-scale spatial variables explained the highest amount of community variance (Collembola: 6%,

317 Carabidae: 14%), while a considerably higher percentage could not be explained by the
318 RDA axes (Collembola: 86.4%; Carabidae: 74%).
319
320 **Discussion**
321 Ecological studies analyzing the effects of land-use changes on local community
322 structure have traditionally focused on aboveground communities, belonging to the
323 same trophic level, and within a well-defined spatial scale (Chase and Bengtsson 2010).
324 However, spatial and ecological processes operate at a hierarchy of spatial scales
325 (Cushman and McGarigal 2002) and their relative influence depends on the spatial
326 range of the targeted organisms (Ettema and Wardle 2002; Berg 2010). Here, we have
327 analyzed changes in community structure across two groups of soil fauna, with a range
328 in body size, life-form and dispersal ability. On the one hand, the small-sized
329 collembolan communities, mainly eu-edaphic and with low dispersal ability, and on the
330 other hand, the carabid beetle communities, which are bigger than collembolans and
331 mainly epigeous, with a higher ability to disperse and colonize new areas.
332 We found that spatial processes were relevantly determining community
333 structure of both taxonomic groups. While carabid communities were spatially
334 structured at a broader scale, reflecting a LW effect, collembolan communities were
335 structured more at fine-grained spatial scales. However, in contrast with carabid
336 communities, both spatial and environmental factors explained only a relatively small
337 amount of community variance of soil eu-edaphic fauna. The effect of environmental
338 factors at different scales was small compared to spatial effects on collembolan
339 community variance. Conversely, environmental factors, especially at the landscape
340 scale, governed carabid community changes along the land-use gradient.

Our first hypothesis, that the relative importance of spatial processes differs between soil arthropods with different dispersal ability, was therefore supported by the observed data. Also, the fact that carabid beetles responded mainly to landscape features across the agro-forest mosaics partly supports our second prediction that environmental factors at coarser spatial scales, namely patch shape and configuration at the landscape scale, more distinctly determine carabid beetle community structure in relation to the eu-edaphic communities.

*Effect of space across groups of soil fauna*

Our results showed that epigeous carabid beetles (sampled by pitfalls), were less affected by distances among habitat patches than eu-edaphic and hemi-edaphic collembolan communities (collected with soil cores). These were still affected by the smallest distances between neighboring plots within landscape windows (LWs). These results suggested that, for collembolans, the distances among neighboring habitat plots, a minimum of 200 meters apart, were already working as a spatial barrier. Presumably the spatial scale of the sampling design of this study was too wide for Collembola (see for example, Aström and Bengtsson 2011). The 4x4 grid of sampling points was not able to capture the real effects spatial and environmental factors determining collembolan community changes, as they show high variability at very fine-grain spatial scales. In fact, the spatial range of edaphic fauna is tuned by high spatial and temporal variation in microhabitat conditions and resource availability at smaller spatial scales (Bengtsson et al. 1994; Chust et al. 2003b; Hedlund et al. 2004). So it is not surprising that home range and dispersal ability of soil-dwelling fauna is much more limited than dispersal ability of surface-dwelling communities (Hedlund et al. 2004; Berg et al. 2010). In line with previous studies (e.g. Thompson and Townsend 2006; van de

366 Meutter et al. 2007; Siqueira et al. 2012) we found that the relative influence of spatial
367 and environmental factors, at a specific spatial scale set up in the sampling design,
368 depends on the spatial range and dispersal ability of the studied taxonomic groups. This
369 outcome should be considered in studies testing the effects of multi-scale ecological
370 processes on multiple taxa within a landscape mosaic, namely ecological studies based
371 on a metacommunity approach (Leibold et al. 2004), weighting the relative effect of
372 spatial and environmental factors at a fixed spatial scale.

373 Even for soil-dwelling communities, the relative importance of spatial distances
374 among local communities might depend on the degree of habitat heterogeneity and
375 complexity within the landscape (Kneitel and Chase 2004). In a precvious study using
376 collembolan communities, sampled not only in woodland habitats but also in open areas
377 (mostly agricultural fields) along the land-use gradient, we found a decrease in the
378 importance of spatial factors relative to environmental factors (Martins da Silva et al.
379 2012) due to the striking contrasting situations such as forest habitats vs. agricultural
380 habitats.

381 The importance of abiotic and biotic conditions for the structuring of soil fauna
382 has been shown in previous works (e.g. Rantalainen et al. 2005; Heiniger et al. 2014).
383 Thus, both spatial distances between patches and the degree of habitat heterogeneity
384 play a role in determining the community structure of soil fauna, although in this study
385 spatial factors ruled out environmental factors because the sampled community
386 assemblages were too distant from each other. Also, the environmental component
387 could have been underestimated simply by missing those environmental variables most
388 relevant to eu-edaphic fauna. Indeed, Collembolan communities are deemed to be
389 structured by strong species sorting across a gradient of soil moisture and organic
390 content, although these variables were not explicitly measured in this study (Hopkin

1997). This limitation should also be taken into account in this comparison between soil-dwelling and surface-dwelling communities, regarding the relative importance of spatial and environmental components.

*Effect of environmental factors at different spatial scales*

Contrary to collembolans, many carabid beetles have the ability to fly (Lövei and Sunderland 1996) or disperse over relatively long distances by active walking (Baars 1979; Niemelä et al. 1992). Spatial distances among sampling plots, within each LW, were not too high to hamper the environmental effects on carabid community changes along the land-use gradient. Still, the importance of shared and pure effects of space at broader scales showed that carabid communities were spatially structured, which could be reflecting an LW effect, i.e., distances among LWs were in part confounded with environmental factors (e.g. management types and landscape configurations of each LW) due to the effect of spatial autocorrelation (Borcard et al. 1992; Smith and Lundholm 2010).

Both spatial and non-spatial models revealed that changes in carabid beetle community structure were mainly governed by environmental conditions at a coarser spatial scale, namely to changes in the arrangement of the landscape mosaic along the land-use gradient. As surface-living communities comprise in general species with a larger body size and wider spatial range, they naturally require broader habitat areas and perceive the habitat differently to soil-dwelling communities (Chust et al. 2003a). For instance, the effects of habitat fragmentation, by creating a more complex configuration of the landscape mosaic, may have a stronger effect on carabid community structure than finer scale changes in local vegetation cover within the same land-use type (e.g. cork-oak habitats). The importance of landscape features on carabid activity, density,

species richness and community composition has been the focus of recent studies (e.g. Barbaro and Halder 2009; Nabe-Nielsen et al. 2010; Sattler et al. 2010; Woodcock et al. 2010; Flohre et al. 2011; Jonason et al. 2013; Lemessa et al. 2014; Puech et al. 2014), although landscape metrics such as patch shape of different land-use types have hardly been addressed. In this study we found that the shape of habitat patches interspersed in the landscape mosaic may provide a clearer understanding about the ecological processes underlying community dynamics and species trade-offs in agro-forest landscapes. For instance, the proportion of good dispersers to poor dispersers, as well as the predominance of generalists over habitat specialist species, may depend on how narrow and convoluted habitat patches are within the landscape mosaic (Hamazaki 1996; Tanner 2003). In this sense, further insight may be gained with studies including community traits related to dispersal power (e.g. macropterous vs. brachypterous species), body size (active versus passive dispersal) or degree of habitat specialization (e.g. Ribera et al. 2001; Brose 2003; Kotze and O'Hara 2003; Niemelä and Kotze 2009). By identifying general patterns of community responses to landscape features, we could have a more comprehensive view on how community assemblages and functional groups are effectively distributed, and to predict how they will cope with current and future land-use changes (Kotze et al. 2011).

*Implications for fundamental and applied ecology*

Soil-dwelling and surface-living communities responded differently to spatial distances among cork-oak habitats along the land-use gradient, and were affected differently by environmental factors acting at different spatial scales. While most soil-dwelling

communities require ecological assessments at the local plot scale, community patterns of epigeous soil fauna, especially of predatory taxa, may be predicted by some features of the landscape, including the shape of forest and open habitat patches interspersed in the agro-forest mosaic. We believe these findings add important insights into recent ecological frameworks, particularly the metacommunity concept (Leibold et al. 2004), which incorporates the relative importance of spatial and environmental processes to explain community patterns in fragmented landscapes. Based on the present results, we suggest that studies testing ecological models should take into account the spatial range of the targeted taxa - not only their dispersal ability, but also the proper spatial scale at which the organisms perceive habitat heterogeneity and respond to changes in local conditions (Chust et al. 2004). The need for multiscale analyses in order to adequately characterize landscape heterogeneity has been highlighted in previous work in the field of landscape ecology (e.g. Wu 2004; Costanza et al. 2011). This notion gains even more importance considering that habitat heterogeneity and landscape patterns might be differently perceived by surface and soil-dwelling organisms, depending on the focal spatial scale of a specific study.

This aspect has also important implications for landscape management and conservation plans in Mediterranean agro-forest mosaics. Particular features of the landscape resulting from traditional management may contribute to determine community structure of different taxonomic groups, and hence monitoring programs for conservation purposes should be scaled at the level of the targeted taxa or functional group. This is in line with previous studies that have suggested that different conservation strategies are needed to protect biodiversity, depending on the particular taxonomic group (e.g. Yaacobi et al. 2007; Lemessa et al. 2014).

In conclusion, our results support that in both theoretical and applied ecological studies with regards to the effects of spatial and environmental processes governing community structure in landscape mosaics, the fields of community and landscape ecology should be integrated. Indeed, the trans-disciplinary nature of landscape ecology has been emphasized by relevant authors in this field (see Wu and Hobbs 2002) and a multiscale approach, as well as the combination of hierarchy concepts (*sensu* Wu and Loucks 1995; Turner et al. 2001) with community ecological frameworks (*sensu* Leibold et al. 2004; Cottenie 2005) could help to improve the ability to predict changes in community structure over space and time.

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**Table 1.** Characterization of the land-use windows (LW1, LW2, LW3 and LW4) selected for this study. At the regional scale, the landscape structure reflected by the main types of land-use and management practices caused different patterns of

vegetation cover among LWs, i.e. higher numbers of closed habitats within LW1 and LW2 in relation to LW3 and LW4.

| | | LW1 | LW2 | LW3 | LW4 |
|---|---|---|---|---|---|
| **Landscape management** | Land-use | natural forest | managed forest | agro-forest | agro-forest |
| | Interventions | none | pruning | pruning/grazing | pruning/grazing |
| | Management level | none | low | low | medium |
| **Nº of sampling plots** | Closed woodland | 8 | 9 | 3 | 4 |
| | Open woods | 3 | 3 | 8 | 6 |
| | Grass/Shrubland | 5 | 3 | 5 | 6 |

494 **Table 2.** R and P-values derived from ANOSIM pairwise comparisons of collembolan
495 and carabid community composition values using the Bray-Curtis similarity index.

| | Collembola | | Carabidae | |
|---|---|---|---|---|
| | R | P-values | R | P-values |
| LW1 vs. LW2 | 0.196 | 0.008 | 0.037 | 1 |
| LW1 vs. LW3 | 0.094 | 0.271 | 0.236 | 0.002 |
| LW1 vs. LW4 | 0.194 | 0.005 | 0.281 | 0.002 |
| LW2 vs. LW3 | 0.184 | 0.021 | 0.327 | <0.001 |
| LW2 vs. LW4 | 0.237 | 0.005 | 0.317 | <0.001 |
| LW3 vs. LW4 | 0.132 | 0.064 | 0.311 | 0.002 |
| Total | 0.175 | <0.001 | 0.247 | <0.001 |

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499 **Table 3.** Selected environmental variables (at plot-patch-landscape levels) obtained
500 from the RDA forward selection procedure performed for each taxonomic group.
501 Detailed descriptions of each variable are provided in Supplementary material Table A1
502 ("Herb" - percentage coverage of herbaceous vegetation; "Density" – "cattle density",
503 "Area Cork" - area with cork production, "Time Cork" - time since last cork removal,
504 "Area Cut" – forest area harvested; "G_NP" –number of grassland patches, "F_Contig"
505 - spatial connectedness, or contiguity, of forest patches, "F_Shape" and "G_Shape" -
506 shape index of cork-oak patches in forest and grassland habitats, respectively, "G_Prox"
507 - proximity of all grassland patches).

| | | | Variables | Order | $R^2$Cum | Adj$R^2$Cum | F | P values |
|---|---|---|---|---|---|---|---|---|
| Collembola | Hab | 1 | Herb | 5 | 0.004 | 0.003 | 2.607 | 0.004 |
| | Man | 1 | Density | 5 | 0.051 | 0.035 | 3.128 | 0.001 |
| | | 2 | TimeCork | 3 | 0.085 | 0.053 | 2.089 | 0.006 |
| | Lan | 1 | G_NP | 10 | 0.051 | 0.035 | 3.106 | 0.001 |
| | | 2 | F_Contig | 7 | 0.089 | 0.057 | 2.400 | 0.006 |
| Carabidae | Hab | 1 | Herb | 5 | 0.088 | 0.072 | 5.586 | 0.001 |
| | Man | 1 | AreaCork | 2 | 0.089 | 0.073 | 5.635 | 0.001 |
| | | 2 | TimeCork | 3 | 0.143 | 0.113 | 3.636 | 0.001 |
| | | 3 | AreaCut | 1 | 0.174 | 0.129 | 2.056 | 0.027 |
| | Lan | 1 | G_Shape | 13 | 0.101 | 0.085 | 6.503 | 0.001 |
| | | 2 | F_Shape | 5 | 0.179 | 0.150 | 5.414 | 0.001 |
| | | 3 | G_Prox | 16 | 0.208 | 0.166 | 2.090 | 0.029 |

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513 **Figures captions:**

514 **Figure 1.** Sampling points (spatial coordinates) of the selected landscape windows
515 (LWs1-4) along the consolidated alluvial plain of the river Tagus (Alcochete). LW1 –
516 unmanaged cork-oak woodland, LW2 – managed closed woodlands, LW3 – managed
517 agro-forest dominated by open woodlands, LW4 - managed agro-forest dominated by
518 open woodlands and pastures (see Table A1 for details on landscape structure among
519 the different LWs).

520

521 **Figure 2.** Average (and SE) of Bray-Curtis similarity values between sampling plots
522 within LWs for the two taxonomic groups (Collembola: white bars; Carabidae: grey
523 bars).

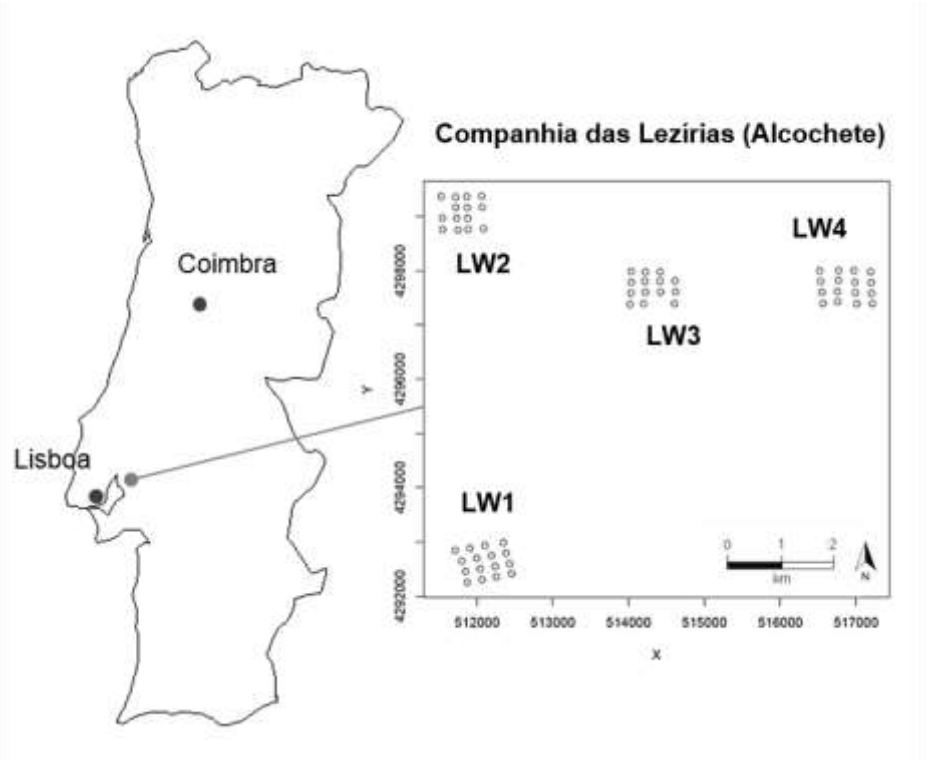
524

525 **Figure 3.** Venn diagrams of variation partitioning for the environmental variables in the
526 non-spatial model, considering habitat ("hab") level, management ("man") level and
527 landscape ("lan") level. Pure and shared effects of the explained % of variance in
528 collembolan and carabid beetle community structure along the land-use gradient. "*"
529 and "**" correspond to the significance levels ($P<0.05$ and $P<0.01$) of the percentage
530 explained by the different environmental predictors.

531

532 **Figure 4.** Venn diagrams of the variation partitioning between the environmental
533 component ("env"), broad-scale and fine-scale space component. Pure and shared
534 effects of the explained % of variance in collembolan and carabid beetle community
535 structure along the land-use gradient. "*" and "**" correspond to the significance levels
536 ($P<0.05$ and $P<0.01$) of the percentage explained by the different spatial (MEMs) and
537 environmental predictors.

**Figure 1:**


Companhia das Lezírias (Alcochete)
Coimbra
Lisboa
LW1
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515000
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517000
X
Y

544 **Figure 2:**

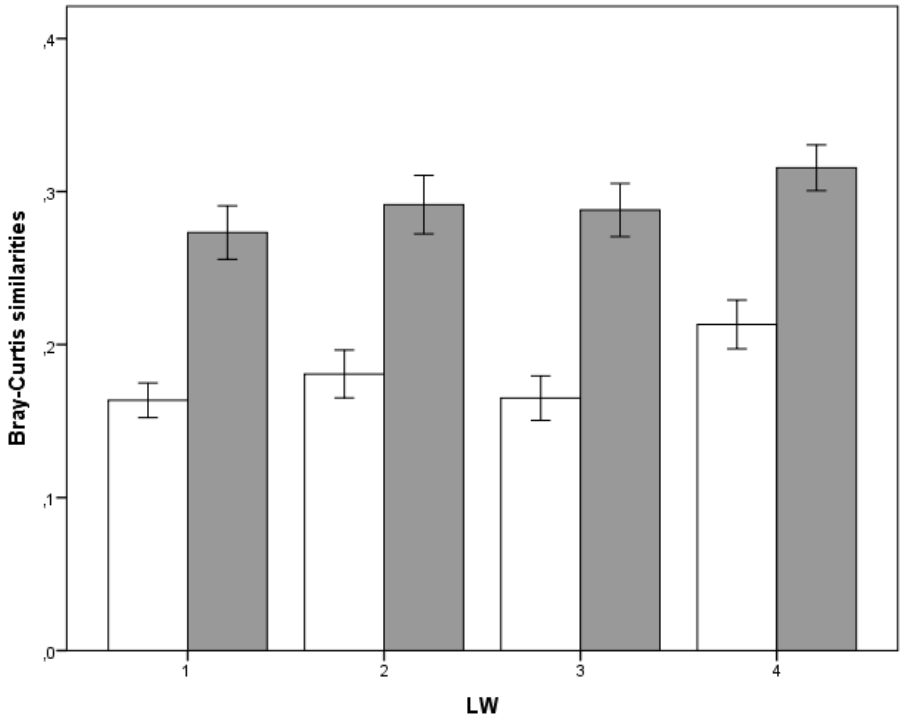


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**Figure 3:**

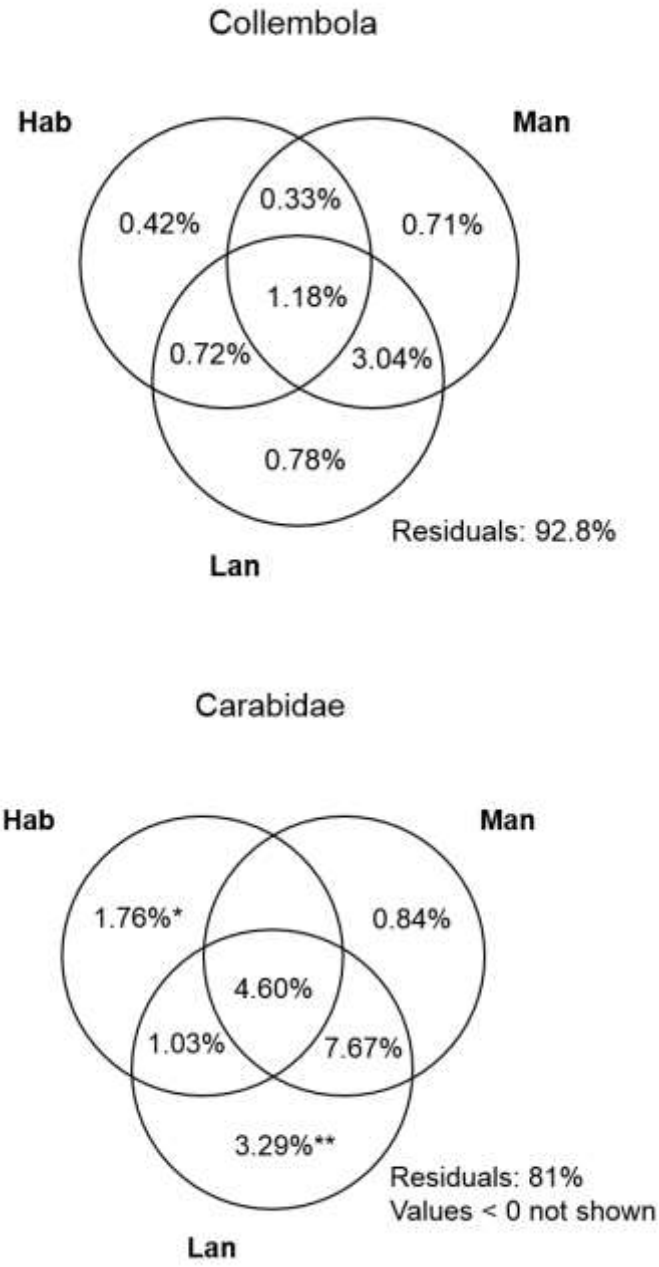
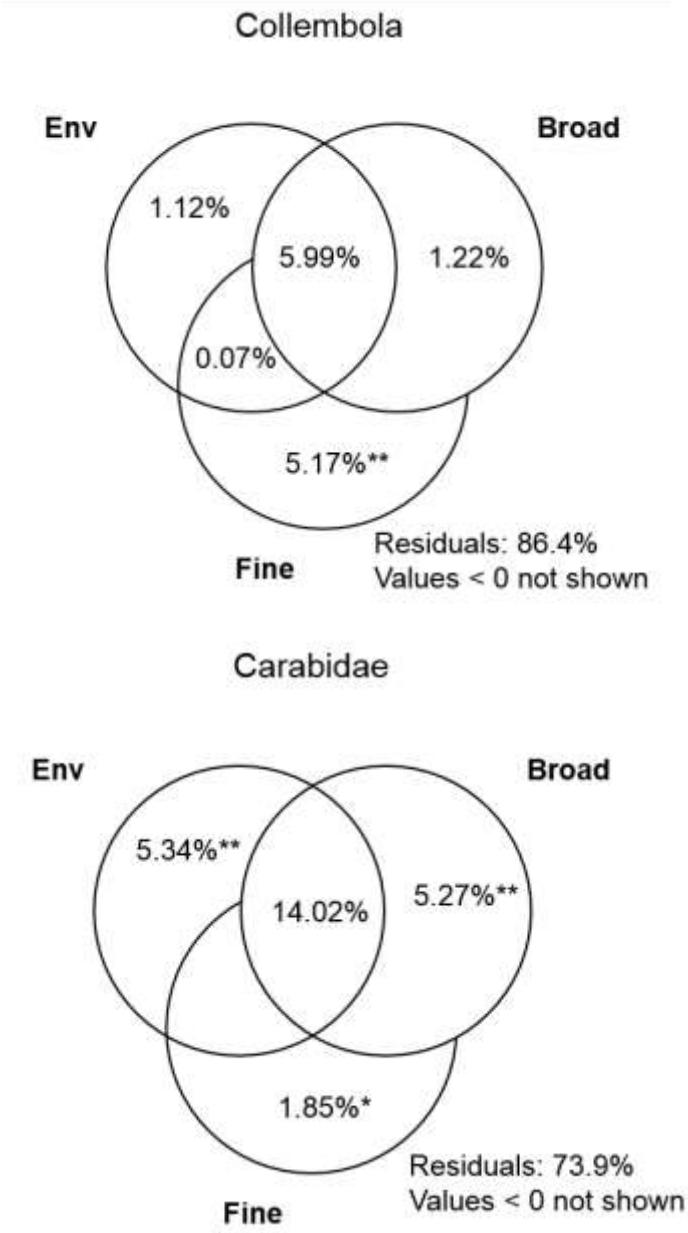

Collembola
Hab
Man
0.42%
0.33%
0.71%
1.18%
0.72%
3.04%
0.78%
Residuals: 92.8%
Lan
Carabidae
Hab
Man
1.76%*
0.84%
4.60%
1.03%
7.67%
3.29%**
Residuals: 81%
Values < 0 not shown
Lan

**Figure 4:**


Collembola
Env
Broad
1.12%
5.99%
1.22%
0.07%
5.17%**
Fine
Residuals: 86.4%
Values < 0 not shown
Carabidae
Env
Broad
5.34%**
14.02%
5.27%**
1.85%*
Fine
Residuals: 73.9%
Values < 0 not shown

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